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aggregates into the resultant energy of organized waves; that the waves which are emitted on the sides of bodies facing each other are more or less neutralized, thus allowing of a greater pressure on the outer sides, and thereby causing the bodies to be driven together. Finally, the theory presented discovers a complete cycle in the transformation of energy. Hitherto the energy dissipated into space has found no explanation for its conservation and return. The theory presented herein recovers that energy in gravity, ready to be again transformed in endless recurrent changes.

A BRIEF OUTLINE OF ECOLOGY.

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An address delivered before the Academy, at Topeka, December 29, 1900.

I have been requested by the Academy to present a paper upon the subject of "Ecology." On account of numerous other duties, I have decided to make this subject the title of the address expected of me this year as retiring president.

The word "ecology" is of recent origin. The word seems to have been first used in 1891, by Strasburger, a German botanist. He says, in his discussion of the subject: "Anpassungslehre oder Öcologie, fälschlich jetzt als Biologie bezeichnet, da auch doch Biologie überhaupt die Lehre von den lebenden Wesen ist." In 1893 the Madison congress considered, among other matters, the terminology of plant physiology. It fell to me, as a member of the committee appointed to formulate suggestions, to present our conclusions upon the subject of ecology. It was recommended that the term "ecology" be used for that part of plant physiology which deals with the adaptive processes of plants, and that it be spelled with an "e" instead of "œ." This recommendation was adopted, and the word has since come into general use. Although the word is of recent origin, the subject itself has received attention for a much longer period. In Germany, it has been known under the name of "biologie," and, for want of a better term, the corresponding English word "biology" has been used in this country. But biology, properly, refers to the science of life, and includes the two branches, zoölogy and botany. Hence this second use of the word produces confusion.

It is difficult to accurately define ecology, as it cannot be easily limited; but, as generally accepted, it includes all that part of physiology in general which deals with the effect of environment upon the plant. Physiology, proper, deals with the action of physical and chemical forces within the plant. A study of the chemical changes connected with nutrition, or the physical forces involved in water absorption, is in the domain of physiology. A study of the methods by which a plant adapts itself to changes in the amount of water or light, or the different soil conditions, is in the domain of ecology. It will be seen that ecology deals with organs and physiology with the cell. But in one-celled organisms or even in little differentiated multicellular organisms this difference becomes reduced to zero. While it is convenient to segregate certain vital phenomena under a separate name, it must not be understood that these phenomena are not brought about by the same forces that are considered in physiology. But physiology deals with its phenomena as identical with phenomena in the physical world, and is constantly trying to reduce these phenomena to their lowest terms; as it were, to coordinate them with similar phenomena observed in the laboratory. To the physiologist the cell forming the root hair is an example of osmosis, and its action can be successfully reproduced in the laboratory. The living protoplasmic membrane is the osmotic membrane; the soil water, a weak solution of

minerals, is on one side and the more concentrated cell sap is on the other. A current is set up from the soil water to the cell sap, and the cell thus absorbs water containing the necessary mineral food. This process, then, is not peculiar to living organisms. In a like manner, the chemist looks upon the synthesis of carbohydrates in the plant as a purely chemical process. While this process has not been reproduced in all its steps by the chemist, yet he, with the botanist, looks upon this as a process which can be carried on independently of the plant.

Now let us examine one or two cases of ecological phenomena. Certain leaves when exposed to too much light twist on their petioles so as to bring the edge of the leaf in the direction of the light; that is, the leaf lies in the plane of the incident rays. They thus escape the injurious effects of the light, and, what is more important, at the same time escape the accompanying heat rays, and thus reduce the evaporation from the leaf surface. This phenomenon, known as "paraheliotropism," is common in plants of the dry regions. The organ in this case responds to a stimulus, and responds in such a way as to protect itself against injury. A plant under these circumstances is said to adapt itself to its environment. A phenomenon of this kind is more distinctly vital. I do not wish to be interpreted as separating vital phenomena as fundamentally different from non-vital. From a philosophical standpoint, I cannot admit that they are; but on account of the extreme complexity of the combinations they are more conveniently studied as combinations. No doubt the phenomena of paraheliotropism is capable of analysis and will be found to be a combination of so-called single phenomena. But it is really this adaptability or mobility in a plant which distinguishes a living thing from a piece of apparatus.

It is not my intention to discuss the fundamental relations of ecology to physics and chemistry, nor to propound a theory of life. Instead I wish to give a brief outline of the subject in its present status. I interpret this as the wish of the Academy when the subject was assigned to me.

During the Linnæan period, and for some time afterward, plants were studied only to be classified. As you all know, the nature philosophy of that day looked upon species as fixed; hence, the chief care of the botanist was to so describe a plant that it could with certainty be distributed into its proper pigeonhole. The descriptions in Linnæus's "*Species Plantarum*" are models of clearness. The pigeonholes are well distinguished. But, alas! the plants so often fail to conform to the descriptions. When considering two closely allied species Linnæus apparently threw into the waste-basket all intermediate forms. Botanists in general seem not to have taken much interest in plants as living organisms. This tendency persists more or less to the present day, but is fast disappearing. Systematic botany holds a prominent position in the various branches of the botanical science; but its study is modified to suit the accepted philosophy of development.

One of the earliest to record systematic observations in ecology was Sprengel, who in 1793 published a little book upon "*The Secret of Nature in the Form and Fertilization of Flowers Discovered*." He laid the foundation of the theory of honey containing flowers, viz.: that the flower secretes nectar to attract insects, sometimes a single species; that the flower is of such a shape that the insect in getting the nectar is compelled to transfer, unconsciously of course, the pollen from the anthers to the stigma. It is a curious fact, however, that Sprengel did not recognize the real reason for all this: that the insects were utilized by the plant to transfer pollen from one plant to another because cross-fertilization is better for the plant than self-fertilization. The result was that Sprengel's ex-

cellent observations were relegated to obscurity by the upper crust of botanists—the systematists who did not care to waste their time on such amateur work.

While ecological observations are scattered here and there through later botanical writings, they lacked coherence, and this branch was constantly handicapped by the theory of the fixity of species. It remained for Charles Darwin to bring order out of chaos and give us a working theory of development. His investigations may be said to have laid the foundation of ecology. It is needless to dwell upon the theory of the Darwinian school, but ecology owes its impetus to the recognition of the plasticity of species. The study of adaptability has been so active and the mass of facts accumulated has been so great that it was recognized as a distinct branch of botanical science, first under the name of biology and later under the name of ecology. Let us now take a look at a brief classification of the subjects included. It will be seen at once that ecology is a study of life relations—the relations of the plant to its environment. The factors which influence the plant from without are known as ecological factors, and may be arranged for the most part in the following groups:

WATER.	AIR.	ANIMALS.
HEAT.	SOIL.	OTHER PLANTS.
LIGHT.		

The fact that a plant thrives where it is shows that it is adapted to the conditions, and that an equilibrium has been established between the plant and the factors normally surrounding or affecting it.

WATER.—Water is a vital necessity. The variation in the water-supply causes corresponding variations in the structure. In submerged plants the water with the containing mineral matter is absorbed directly. Hence there is no transpiration current, and the roots have no absorptive function. Roots when present are fastening organs. If the leaves are floating or emerged there is set up a transpiration current which must be supplied from beneath by the absorptive action of the roots. In all land plants a transpiration current is necessary to supply the mineral matter from the soil. It is not often that the soil conditions and air conditions are so evenly balanced that the plant is free to take up and evaporate all the water it needs for the most rapid growth. In some cases, on account of the saturated atmosphere, there is danger from a stagnated transpiration current, and the plant endeavors in various ways to aid evaporation. Experiments have shown that an individual plant can be profoundly modified by a change in the water relation. A normally xerophytic plant with rosette foliage can be made to stretch out its axis, to broaden its leaves, and otherwise take on the structure of a hygrophyte. To indicate the nature of the problems presented I will suggest a few adaptations, some proved by experiment, others still hypothetical. In the rain forests of the tropics the leaves are often provided with long points and converging veins to lead off the water easily. Mottled leaves in which irregular areas lack chlorophyll increase the evaporating surface without increasing that engaged in photosynthesis. The presence of the red coloring matter on the under surface of floating leaves may be for the purpose of converting the waste light into heat, thus slightly raising the temperature of the leaf and enabling it to evaporate, when otherwise the air would be saturated and prevent evaporation. Glands which excrete liquid water are common. On the other hand, in dry regions the plant is obliged to prevent evaporation as much as possible, without entirely suppressing the transpiration current. There are numerous and curious methods by which plants protect themselves from drought.

HEAT.—Plants are rarely injured by the high temperature to which they are subject in nature, provided the water-supply is not reduced. But, except in the

tropics, they are likely to be subjected to low temperature, to which they must become adapted in order to live. No plant can vegetate at a temperature below freezing, but by proper adaptation many plants can endure an indefinitely low temperature in the resting stage. In high latitudes it becomes a question of ability to endure the long winter. Plants have been found as far north as soil conditions have permitted their growth. At high altitudes, however, vegetation is limited by the lack of a growing season. The temperature may remain throughout the year below the point at which growth is possible. Under this head, then, is the study of the methods of resisting injury from low temperature.

LIGHT.—Too intense light is injurious, while with too little light the process of photosynthesis cannot be carried on. By assuming the profile position, either temporarily, as in motile leaves, or permanently, as in compass-plants, with vertical leaves, injury from too intense light can be avoided. Others must exert themselves to obtain the maximum amount of light. Some plants bring the leaves into the maximum light position by heliotropic movements. Submerged water-plants and the shade plants of dense forests are obliged to adapt themselves to the minimum amount of light for growth.

AIR.—Aside from the indirect effect upon transpiration, the air relations of plants may be divided into about three groups: (1) The supply of oxygen for the purpose of respiration, which is necessary to all active cells. Interesting adaptations are found in swamp plants for leading air down to the roots: aerating tissues, air canals, cypress knees, etc. (2) The direct mechanical effect of wind upon the plant body. (3) The methods by which plants utilize air-currents for the dispersal of seeds and pollen.

SOIL.—Soil relations may be chemical or physical, the latter being by far the most important. The elements necessary for plant growth are usually present in cultivated soil in sufficient amount, and, usually, there is nothing in the soil which is of direct injury. The physical condition of the soil is chiefly concerned with the water relation. When the soil contains a large amount of soluble salts plants have difficulty in absorbing sufficient water; and when the soil water is as concentrated as the cell sap, plants cannot exist. Such conditions obtain in salt marshes, alkali plains, etc. And the plants are of a pronounced xerophytic type, from the necessity of reducing transpiration to suit water-supply.

ANIMALS.—Animals use plants for food, and they inflict injury by tramping upon them. Hence, protective devices in the shape of thorns and prickles, or a bitter or irritating sap, and the rosette habit. Insects aid in the pollination of flowers; a study of which is an important branch of ecology. Animals aid in the dispersal of seeds, by accidentally carrying those which have devices for attachment, or by eating the fruits, in which the large seeds are thrown away and the small ones escape digestion. Special relations which are extremely interesting occur between ants and plants. Certain leaf-cutting species of ants cultivate a kind of fungus in their underground nests. The leaves are gathered to furnish a substratum for the fungus, which, in its turn, yields a peculiar fructification upon which the ants feed. Other species, enemies to the preceding, are retained as guards by several kinds of plants, which thus escape denudation. These plants furnish especially formed homes, and often also food for their protectors. The homes and special-food bodies appear to have no other function than that of inducing the guards to take up their abode there and recompensing them for their trouble.

OTHER PLANTS.—Every individual, from the time it is cast loose from the mother plant as a seed, must struggle against the various factors mentioned, but

its severest battles are those against other plants, which compete with it for soil, light and water. And the competition increases with the closeness of the genetic relationship. There is always an appreciable probability that a plant may find a niche in nature where it can avoid competition from other species, but it is a very rare exception when a plant can escape competition from other individuals of the same species.

So far we have taken a cursory view of the ecological factors. We will now turn to another branch of ecology, which may be called ecological plant geography. It might be called the distribution of plant societies.

Plants may live together and bear to each other several kinds of relationship. The competition for light has developed a physiological class of plants called lianas, or climbers, which use other plants as their support, and hence escape the necessity of forming a self-supporting trunk. Epiphytes are plants which use others as a substratum upon which to grow, but are not parasitic. They are usually xerophytic in their structure, and have developed many curious contrivances for catching and holding rain-water. Saprophytes derive their organic food, more or less elaborated, from the partially decomposed vegetable debris. Parasites absorb their food, or a part of it, directly from the living cells of their host. In certain cases, as in lichens, there is the relation of master and slave (helotism). Certain fungi derive their nourishment from simple forms of algæ, but nevertheless protect them, the whole organism (lichen) having a definite structure, depending upon the species of fungus and alga involved. The most common relation, however, is that in which different species of plants compete with each other for existence under the same conditions. This relation has received the name "commensalism." A study of these relations has given rise to the branch of ecology known as ecological plant geography. The plants which live under similar conditions have a definite physiognomy, and are called a plant society, or rather, more commonly, a formation. Where the conditions have remained practically the same for a period sufficient for an equilibrium to be established, the species have become adapted to the conditions, including the tendency of the individuals to encroach upon each other. Thus, a plant society is defined as being those individuals which exist together under a given set of conditions. There have been attempts to classify societies into four large groups: Hydrophytes, those living in water or where the soil is saturated with water; xerophytes, those living in more or less arid situations and where the plants must resist evaporation; mesophytes, where the conditions are medium so far as water-supply is concerned; halophytes, where there is an excess of salts in the soil. The division is, however, not satisfactory. Swamp plants would be classed among the hydrophytes; yet they possess undoubted xerophytic characters, such as vertical leaves, reduced surface, thick epidermis, etc. Swamp plants must resist evaporation at times, when, on account of the cold, wet soil, the roots are not active enough to supply the transpiration current. Schimper, a recent writer on this subject, attempts to divide plants into hygrophytes, those on which the transpiration current must be aided; xerophytes, in which the transpiration current must be hindered; and tropophytes, in which there is an alternation of these two sets of conditions. Like all classifications, it has holes in it. It is more satisfactory to classify on the basis of adaptations, and recognize certain ones as xerophytic and others as hydrophytic. Many of our deciduous trees may be classed among the mesophytes, yet they have the very prominent xerophytic character of dropping their foliage on the approach of winter. In another paper I have discussed the ecological plant geography of Kansas. The xerophytic flora predominates, the chief societies being prairie flora, flora of the sand-hills,

and flora of stony hills. The hydrophytic societies occur in and near our water-courses, ponds, sloughs, marshes, and springs. The mesophytic societies are confined to the border-land between the hydrophytes and xerophytes, and more especially in the shade of the lowland woods. The halophytes are found in the salt marshes which occur through the interior of the state.

Although, while the conditions remain unchanged, the societies remain in an equilibrium, there is, nevertheless, what might be termed a conflict of societies going on everywhere. As soon as the conditions change, even slightly, one society will gain an advantage over its neighbors. There seems to be little doubt that the forest societies are gradually encroaching on the plains. It must not be inferred that every species is found where are conditions best suited for its development. It is, rather, that each species is found where it can best compete with others able to endure the same conditions. For example, in Kansas the red cedar is found on barren limestone cliffs, and presents a gnarled and more or less stunted aspect. Yet, under favorable conditions—that is, ordinary rich soil—it produces a vigorous and symmetrical body. The same is true of the bald cypress of our Southern states. It is found native in swamps, and usually is flat topped and stunted in its growth, with a much less vigorous aspect than specimens cultivated in moderately dry soil. It would appear that they have been unable to compete in those localities where they could thrive best, but have been forced to take refuge in the stony hills, in the one case, and the swamps in the other, where they can maintain themselves against their competitors. So we see that there is a constant struggle between individuals in a society, and between societies in a given area or region.

Ecology also includes the wider class of distribution ordinarily called the geographical distribution of plants; that is, the distribution of plants on the earth's surface into zones, regions, and areas. The division into zones is based on climatic conditions. There are four zones: tropical, temperate, arctic, and mountain. The regions are subdivisions of these zones of sufficient extent to eliminate the effect of local conditions. As examples, may be mentioned the great plains and the Arizona-Mexico desert region of North America, the steppes of Russia, and the pampas of South America. This study includes not only the actual distribution of plants upon the earth's surface, but also the causes which lead up to it, in so far as they are concerned with adaptation. Thus, we have the difficult problem of the origin and relations of the flora of a particular region. The conditions have not always been as they are now; but, under the influence of those mighty forces which have fashioned our continents, islands, mountains, and lakes, an indefinite number of changes have taken place in the relations and composition of the plant societies. Vast forests once flourished where is now a wide expanse of prairie. Palms inhabited the polar circle and arctic plants were spread broadcast over the temperate regions. Floral areas have had their rise and fall. First one species is dominant, then another. You are all familiar with the distribution of our arctic plants: how, in preglacial times, a more or less tropical flora surrounded the pole; how the oncoming cold drove all vegetation southward; how a modified vegetation followed the retreating glaciers, but left arctic representatives stranded on the high mountain tops of the whole northern hemisphere; how Greenland is so remarkably poor in species compared with other lands in the same latitude, because most of its flora was driven southward into the ocean; how the flora of eastern United States resembles more closely that of Japan and eastern Asia than it does that of California, because a similar flora found similar conditions in these two

regions and could successfully compete; but that portion which was driven down the western coast of North America came in contact with a flora better suited to the conditions, and so was exterminated, with exception of such relics of the past as the grand sequoias, which, however, cannot long survive. I might go on indefinitely with a tiresome enumeration of facts, but I think I have given enough to indicate, in a general way, the scope of ecology.